Z. Säugetierkunde 54 (1989) 347–359

ISSN 0044-3468

Electromorphic variation in selected South American Akodontine rodents (Muridae: Sigmodontinae), with comments on systematic implications

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Receipt of Ms. 15. 3. 1988

Abstract

Phylogenetic relationships among 13 species and 5 genera of South American muroid rodents of the Tribe Akodontini were examined by gel electrophoresis of 26 protein loci. The major findings include: 1. The genus *Microxus,* as represented by the type species *mimus,* cannot be distinguished from taxa of *Akodon* (subgenus *Akodon*). 2. *Bolomys,* as represented by the type species *amoenus,* is only slightly differentiated from *Akodon* (s. s.) and *Microxus* in both genetic distance and the number of uniquely defining alleles. 3. *Akodon (Chroeomys) jelskii* is very distinct from all other akodontines, with unique alleles at 9 of the 26 loci examined; it cannot be considered a close relative of *Akodon* (s. s.) and should be recognized at the generic level. And 4. *Lenoxus apicalis* is the most divergent akodontine with unique alleles at half of the loci studied; it does not form a clade with *Oxymycterus* as has been suggested by some authors.

Introduction

South American sigmodontine rodents (sensu Reig 1980) form a large array of some 50 genera and 200 species (Honacki et al. 1982) that presumptively comprise a single adaptive radiation (Hershkovitz 1962; but see Carleton 1980). These taxa have been grouped into seven or eight tribal categories (Hershkovitz 1962, 1966; Reig 1980, 1986, 1987; Vorontsov 1959) defined on a variety of craniodental, external, and soft anatomical features. Despite the diversity of recognized forms and the clarity of relationships suggested by the formal tribes, few of these taxa have been revised since their initial description, and groups are defined by few poorly studied and often contradictory characters. Much of our ignorance is due directly to the diverse nature of the group as a whole and to the fact that many taxa are known from but a few existing specimens. As a result, most studies have been forced to ignore many taxa except at the most superficial level, and the construction of well-supported phylogenetic hypotheses has been minimal at best. Students working on this general group of rodents have been forced to limit their perspectives to only selected members of any given tribe, or even species within any given supraspecific assemblage.

The Tribe Akodontini comprises one of the major subdivisions of the Sigmodontinae, as recognized by virtually all prior authors. This group is largely distributed through temperate South America and the Andean highlands, but members extend into the southern and western margins of the Amazon Basin and throughout the coastal and interior regions of southeastern Brazil. This is the group of interest to us in this report, and we follow for convenience Reig (1986, 1987) for its memberships (see Table 1).

The present paper defines relationships among selected generic or subgeneric units of this tribal group based on biochemical (= electromorphic) characters. In so doing, however, our data base suffers in the same way as that of all previous workers on neotropical sigmodontine rodents: less than one-half of the currently recognized supra-specific taxa of akodontines and fewer than one-third of the recognized species are

Table 1. **Supraspecific groups of akodontine rodents and number of recognized species (in parentheses) after Reig (1986)**

Taxa examined in this report are indicated by+

Tribe Akodontini
- genus *Akodon* (34)
  - subgenus *Akodon* (25)+
  - *Abrothrix* (6)
  - *Deltamys* (1)
  - *Hypsimys* (1)
  - *Chroeomys* (1)+
- genus *Oxymycterus* (9)+
  - *Bolomys* (6)+
  - *Chelemys* (4)
  - *Microxus* (3)+
  - *Notiomys*[1] (2)
  - *Blarinomys* (1)
  - *Podoxymys* (1)
  - *Lenoxus* (1)+
  - *Juscelinomys* (1)

[1] Pearson (1984) placed *N. valdivianus* in the monotypic genus *Geoxus* separate from *N. edwardsi.*

represented (Table 1). Thus, while we can provide some insights into the relationships among the taxa included herein for analysis, the more general questions regarding both the validity of an akodontine radiation separate from the other sigmodontine groups, as well as the secure placement of supraspecific taxa within the akodontines, must await more complete analyses.

Materials and methods

Tissue samples from 349 specimens representing six supraspecific taxa and 13 species of akodontine rodents were analyzed by horizontal starch-gel electrophoresis. These included seven species usually allocated to the nominant subgenus of *Akodon (aerosus baliolus, boliviensis, mollis, puer, subfuscus, torques,* and a unnamed form from central Peru); one species each of *Chroeomys (jelskii), Bolomys (amoenus),* and *Microxus (mimus);* the monotypic *Lenoxus apicalis,* and two species of *Oxymycterus (hiska* and *paramensis);* see Specimens Examined, below. The species representative of the taxa *Bolomys* and *Microxus* are the type species for those forms. Diagnoses and definitions of specific units recognized, particularly of those named forms usually associated with *Akodon "boliviensis"* (i. e., *boliviensis, puer,* and *subfuscus*), will be published separately.

Twenty-one enzymes and other proteins encoded by 26 presumptive structural gene loci were examined for all populations and taxa. Aqueous extracts of kidney were used for all systems examined. Alleles are designated by their mobility relative to the most common allele at each locus, which was set at 100. The enzymes and other proteins examined and the gel running conditions are given in Table 2. Estimates of genetic divergence of taxa were made using the distance measure of Rogers (1972). Patterns of phenetic similarity among taxa were examined by UPGMA clustering (Sneath and Sokal 1973); phylogenetic trees were constructed by the Wagner distance algorithm (Farris 1972), based on Rogers' D, and from individual character state matrices. Estimates of genic heterozygosity were obtained from the electromorphic genotypes by direct count and averaged across loci for population estimates of individual variability. All calculations of genetic distance and variability measures were performed using the BIOSYS-1 program (Swofford and Selander 1981) on an IBM 4341 mainframe computer, as were construction of UPGMA and Wagner trees. Cladistic analysis of character state matrices, based on the principle of maximum parsimony, was performed using PAUP (version 2.4; Swofford 1985) run on an IBM-PC/XT. In one set of analysis, loci were treated as characters and the observed allelic combinations within taxa were considered the states (following the rationale of Matson 1984, and Buth 1985; see example by Miyamoto 1983). In a second set of analyses, coding was by allelic state, with major alleles at each locus coded separately from minor ones. In the latter case, when no second allele was present in a given taxon, that state was considered as missing. Multistate characters in both analyses were treated as unordered rather than assuming a particular transformation series. Global branch swapping and the MULPARS option were used in PAUP to insure that all possible minimum length trees were found and examined. Wagner trees and those generated from PAUP were rooted either at the mid-point of the greatest patristic distance, or by using a combination of taxa designated as out-groups.

Specimens examined

All specimens are catalogued into the collection of either the Museum of Vertebrate Zoology, University of California (MVZ), or the Museum of Zoology, University of Michigan (UMMZ), as indicated.

Akodon (s. s.) – *aerosus baliolus:* Peru: Depto. Puno; [1] 4 km NE Ollachea, 2380 m (n = 44; MVZ); [2] 11 km NE Ollachea, 1880 m (n = 44; MVZ); [3] Abra Marracunca, 14 km W Yanahuaya, 2210 m (n = 28; MVZ). *boliviensis:* Peru: Depto. Puno; [4] 12 km S Santa Rosa [de Ayaviri], 3960 m (n = 19; MVZ). [5] 4.5 km W San Anton, 4000 m (n = 25; MVZ; [6] 6 km S Pucara, 3850 m (n = 14;

Table 2. **Enzymes and gel running conditions for samples of the akodontine rodents *Akodon* (s.s.), *Akodon (Chroeomys), Bolomys, Microxus, Lenoxus,* and *Oxymycterus***

Enzyme	Enzyme Commission Number	Locus Abbreviation	Electrophoretic Conditions[a]
Glycerol-3-phosphate dehydrogenase	1.1.1.8	Gpd	TC-8[2]
Sorbitol dehydrogenase	1.1.1.14	Sordh	TC-8[2]
Lactate dehydrogenase	1.1.1.27	Ldh-1, -2	TC-8[1]
Malate dehydrogenase	1.1.1.37	Mdh-1, -2	TC-8[2]
Malic enzyme	1.1.1.40	Me	TC-8[1]
Isocitrate dehydrogenase	1.1.1.42	Icd-1, -2	TC-8
6-phosphogluconate dehydrogenase	1.1.1.44	6Pgd	TM
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	Gapdh	TC-8[3]
Glutamate dehydrogenase	1.4.1.3	Gd	TM
Nadh-dehydrogenase	1.6.99.3	Nadh-dh	TC-8
Superoxide dismutase	1.15.1.1	Sod	TC-8[3]
Purine nucleoside phosphorylase	2.4.2.1	Np	LiOH
Aspartate aminotransferase	2.6.1.1	Got-1, -2	TC-8[1]
Creatine kinase	2.7.3.2	Ck-1, -2	TC-8[1]
Phosphoglucomutase	2.7.5.1	Pgm	PGI Phos
Peptidase	3.4.11	Pep-D[b]	Poulik
Peptidase	3.4.11	Pep-B[b]	Poulik
Adenosine deaminase	3.5.4.4	Ada	PGI Phos
Mannose-phosphate isomerase	5.3.1.8	Mpi	TC-7
Glucose-phosphate isomerase	5.3.1.9	Gpi	PGI Phos
Albumin	—	Alb	LiOH

[a] TC-8[1] – Tris-Citrate, pH 8.0, 130 v, 4 hr
TC-8[2] – Tris-Citrate, pH 8.0, 130 v, 4 hr, NAD added to gel
TC-8[3] – Tris-Citrate, pH 8.0, 130 v, 4 hr, NAD and 2-mercapto-ethanol added to gel
TC-7 – Tris-Citrate, pH 7.0, 180 v, 3 hr
LiOH – Lithium Hydroxide, pH 8.1, 300 v, 3 hr, glycerine added to gel
PGI Phos – PGI Phosphate, pH 6.7, 130 v, 4 hr, NADP added to gel
Poulik – "Poulik" system of SELANDER et al. (1971), adjusted to pH 9.1, 250 v, 3 hr
TM – Tris-Maleic Acid EDTA, pH 7.4, 100 v, 4 hr.
[b] Pep-D = phenylalanine-proline substrate; Pep-B = leucine-glycine-glycine substrate.

MVZ). *mollis:* [7] Peru: Depto. Junin; 16 km E Palca, 2540 m (n = 16; MVZ). *puer:* Peru: Depto. Puno; [8] 12 km S Santa Rosa [de Ayaviri], 3960 m (n = 6; MVZ); [9] 6 km S Pucara, 3850 m (n = 23; MVZ); [10] 3.6 km W Munani, 3950 m (n = 5; MVZ). *subfuscus:* Peru: Depto. Cusco; [11] 32 km NE Paucartambo, 3140 m (n = 10; MVZ, UMMZ); [12] 20 km N Paucartambo, 3580 m (n = 10; MVZ); [13] Depto. Puno; 6.5 km SW Ollachea, 3350 m (n = 35; MVZ). *torques:* [14] Peru: Depto. Cusco; below Abra Malaga, 90 km SE Quillabamba, 3450 m (n = 13; MVZ, UMMZ). sp.?: [15] Peru: Depto. Junin; 22 km NE La Oroya, 4040 m (n = 7; MVZ).

Akodon (Chroeomys) jelskii: Peru: Depto. Junin; [16] 22 km NE La Oroya, 4040 m (n=3; MVZ); Depto. Puno; [17] 12 km S Santa Rosa [de Ayaviri], 3960 m (n=1; MVZ); [18] 4.5 km W San Anton, 4000 m (n=3; MVZ); [19] 6.5 km SW Olachea, 3350 m (n=15; MVZ).

Bolomys amoenus: Peru: Depto. Cusco; [20] 20 km N Paucartambo, 3580 m (n=1; MVZ); Depto. Puno; [21] 12 km S Santa Rosa [de Ayaviri], 3960 m (n=7; MVZ).

Microxus mimus: Peru: Depto. Puno; [22] Agualani, 9 km N Limbani, 2840 m (n=7; MVZ); [23] Abra Marracunca, 14 km W Yanahuaya, 2210 m (n=2; MVZ).

Oxymycterus hiska: Peru: Depto. Puno; [24] Abra Marracunca, 14 km W Yanahuaya, 2210 m (n=3; MVZ).

Oxymycterus paramensis: Peru: Depto. Cusco; [25] 55 km N Calca (by road), 3560 m (n=2; UMMZ).

Lenoxus apicalis: Peru: Depto. Puno; [26] Abra Marracunca, 14 km W Yanahuaya, 2210 m (n=6; MVZ).

Results

The purpose of this paper is to examine patterns of electromorphic variation among taxa assignable to the akodontine group of Neotropical cricetid rodents; it is not our intention to describe in detail such variation as we know exists within species over their sampled geographic ranges. As a consequence, the measures reported below, and in the accompanying tables, are summaries averaged across the population samples of each species for which we have data (see Specimens Examined, above).

Variation within taxa

Values for the average number of alleles per locus (A), percent of loci polymorphic per population (P), and proportion of loci heterozygous per individual per population sampled (H) are provided in Table 3. The average species of akodontine rodent examined in this

Table 3. **Measures of electromorphic variability within 13 species and six supraspecific taxa of akodontine rodents**

Taxon	N_p	N_i	A	P	H
Akodon (Akodon) aerosus	3	116	1.2	11.0	0.022
boliviensis	3	58	1.3	20.9	0.067
mollis	1	16	1.2	15.4	0.026
puer	3	34	1.3	21.3	0.069
subfuscus	3	55	1.2	16.1	0.055
torques	1	13	1.1	7.7	0.042
sp.	2	9	1.1	7.7	0.011
weighted average			1.2	15.0	0.043
Akodon (Chroeomys) jelskii	8	34	1.2	15.2	0.071
Bolomys amoenus	2	8	1.1	10.5	0.024
Microxus mimus	2	9	1.0	3.0	0.009
Oxymycterus hiska	1	2	1.1	11.5	0.038
paramensis	1	3	1.0	3.8	0.038
Lenoxus apicalis	1	6	1.1	7.7	0.013
grand mean			1.15	11.68	0.0373

N_p = number of populations; N_i = number of individuals; A = average alleles per locus; P = percent loci polymorphic (95 % criterion); and H = proportion of loci heterozygous per individual.

report is polymorphic at 11.68 percent of its loci, and the average individual is heterozygous for 3.73 percent of its loci. These are somewhat lower values than are typical for rodents as a group (see reviews by Nevo 1978; Nevo et al. 1984). Nevertheless, there is a wide variance in these values across all taxa examined, with P and H values varying from 3.0 to 21.3 and from 0.9 to 7.1 percent, respectively. In general, species of *Akodon* (s.s.) exhibit more variability on average than do those of other genera, and within *Akodon*, those species inhabiting the Altiplano (*boliviensis puer*, and *subfuscus*) exhibit about twice the degree of variability within populations as do those occurring on the eastern forested slopes of the Andes (*aerosus, mollis*, and *torques*; see Table 3).

Differentiation among taxa

A summary of genetic differentiation within and among suprageneric taxa of akodontine rodents is presented both as a matrix of Rogers' genetic distances (Table 4) and as a list of

Table 4. **Matrix of Rogers' genetic distances (DR; Rogers 1972) among populations and taxa of akodontine rodents**

	AAab	AAb	AAm	AAp	AAs	AAt	AAsp	ACj	Ba	Mm	Oh	Op	La
A(A)ab	.023	.090	.097	.125	.113	.141	.141	.530	.304	.128	.424	.436	.566
b		.027	.162	.148	.151	.190	.188	.531	.297	.174	.416	.455	.597
m			——	.197	.178	.081	.211	.539	.305	.188	.402	.431	.538
p				.030	.083	.231	.160	.516	.344	.201	.421	.403	.570
s					.035	.225	.173	.521	.344	.191	.423	.408	.568
t						——	.242	.497	.305	.250	.403	.447	.584
sp.							——	.571	.410	.226	.452	.458	.657
A (C) j								.075	.492	.548	.551	.636	.764
Ba									.014	.346	.350	.464	.635
Mm										.060	.438	.435	.576
Oh											——	.337	.639
Op												——	.645
La													——

Average distances among populations of a single species are given on the diagonal where more than one sample was examined

uniquely defining alleles per taxon (Table 5). The major conclusions obvious from these data are the following:

1. The samples of populations of any single species are relatively homogeneous across geography (Table 4). These values are typical of infraspecific differentiation observed for most species of cricetid rodents (Avise 1976; Avise and Aquadro 1982). For example, the samples of *A. (C.) jelskii* encompass the entire geographic range of this species in Peru, including several very well-marked subspecies (see Sanborn 1947), yet the degree of genic differentiation is small (mean D_R = 0.075 ± 0.004 standard error; Table 4). Nonetheless, with the limited sampling available, substantive differences do exist in the comparison of differentiation among samples for species inhabiting virtually the same geographic ranges. For example, the samples of *A. aerosus baliolus* come from the middle elevation tributaries of the Rio Inambari in southeastern Peru, while those of *Microxus mimus* come from the upper parts in the same drainage. The latter taxon, however, exhibits nearly three times the degree of differentiation among populations as does the former (D_R = 0.060 versus 0.023 ± 0.003 standard error; Table 4).
2. The differentiation that is present between most pairs of *Akodon* species, including *Microxus*, is due to fixed differences for alleles that are otherwise broadly distributed among the total set of species examined in this group. For example, sympatric *boliviensis* and *puer* are distinguished by the GOT-1^{100} and GOT-$1^{162,131}$ alleles, respectively. However, *aerosus, mollis, torques,* and *Microxus* all share the 100 allele, and *subfuscus* shares both 162 and 131 alleles. On the other hand, *boliviensis* and *puer* share the PGI^{167} allele while the others, including *Microxus*, have the 100 allele (Table 5).
3. Differentiation among sampled species within the supraspecific taxon *Akodon* (s.s.) is relatively slight. The average distance among all populations of the seven species is 0.158 (range 0.081–0.242, see Table 4). With the single exception of the unnamed species from central Peru, no alleles are uniquely fixed for any of these species (Table 5). On the other hand, the two species of *Oxymycterus* are strongly differentiated, with D_R = 0.337 (Table 4). Five uniquely fixed alleles in *O. paramensis* and the two in *O. hiska* are responsible for most of this measured distance (Table 5).
4. Not all of the currently recognized genera (Honacki et al. 1982; Reig 1987) are composed of genically uniform and similar species relative to others. For example, *Microxus mimus* is much more similar to *Akodon* (s.s.) than is *Akodon (Chroeomys)*

Table 5. **Alleles segregating at 26 electromorphic loci for 13 taxa of akodontine rodents**
Alleles are identified by relative mobility, as measured from the origin, with the common allele set at 100

Locus	*Akodon (Akodon)*						Species	*(Chroeomys)*	*Bolomys*	*Microxus*	*Oxymycterus*		*Lenoxus*
	aerosus	*boliv.*	*mollis*	*puer*	*subfuscus*	*torques*		*jelskii*	*amoenus*	*mimus*	*hiska*	*paramensis*	*apicalis*
Ldh-1	100	108, 100	100	100	100	100	100, 92	100	100	100	100	100	100
Ldh-2	100, 82	100	100	100	100	100	100	111	100	100	79	100	100
Ck-1	100	100, 74	100	100	100	100	132	100	100	100	100	100	100
Ck-2	100	100	100	100	100	100	100	143, 100	100	100	100	43	100
Got-1	100	100	100	162, 131	162, 131	100	131	108	100	100	123	142	85
Got-2	100, 43	100	100	100	100	100	100	86	100, 71	100	100	100	100
Icd-1	105, 100	100	144, 100	100, 82	118, 100	127, 100	77	109, 86	100	100	91	91	91
Icd-2	100	100	100	100	150, 100	100	100	100	100	100	100	100	108
Mpi	100, 76	100	100	124, 100 88	124, 100	100	100	129, 100	124	100	135, 100	100	153
Gpd	100	100, 71 57	121	100, 91	100, 57	121	100	43	121	100	121	157	78
Mdh-1	112, 100	100	100	100	100	100	100	100	100	100	100	100	100
Mdh-2	100	100, 33	100	100	100	100	100	89	100	100	100	100	100
Sdh	100, 21	100	100	100	100	100	100	100, 29	100	100	100	100	14
6Pgd	100	117, 100	100	100	100	100	100	117, 100	100	100	100	100	108
Pgi	100	167, 100	100, 67	167, 100	100	100	100	67, 17	100, 67	100	67	100	83
Ada	100, 88	100, 88 77	100, 88	100, 88 77	100, 88, 77	100	107, 100	112	97	107, 100	100, 87	81	95, 86
Pgm	138, 100	150, 100	100	100	150, 100, 75	100	100	100, 63	100	100	100	100	100
Sod	100	100	100	100	100	100	100	100	100	100	100	100	100
Ga3Pdh	163, 100	100	163	100	100	163	100	75	100	100	100	100	163
Np	100, 75	100, 63	100	100, 63	100	75	100	100, 75, 38	112	100	112	112, 88	100, 75
Alb	100	100	100	100	100	100	100	94	106	94	106, 103	106	91
Gd	100	100	100	100	100	100	100	100	100	110, 100	100	100	105
Nadh-dh	100	157, 100	100	157,100	157, 100	100	100	171	100	100	14	14	143
Me-2	100	122, 100	117, 100	100	100	100	100	100	100, 78	72	111	111	144
Pap	100	100	100	100	100	100	100	100	100	100	100	107	113
Lgg	100	100	100	100	100	100, 75	100	91	91	100	93	93	93
Total # alleles	36	39	30	36	36	28	28	35	29	28	29	27	28
Total unique alleles	7	4	2	2	3	2	3	16	3	2	5	6	14
Total unique fixed	0	0	0	0	0	0	2	9	1	1	2	5	13[a]

[a] Unique, but polymorphic alleles at single loci counted as one.

jelskii by a factor of over two (mean *Microxus-Akodon* D_R = 0.194 whereas *Microxus-Chroeomys* = 0.529 and *Akodon-Chroeomys* = 0.548; Table 4).

5. Moreover, the subgenus *Chroeomys* is more strongly differentiated from *Akodon* (s.s.) than is *Bolomys amoenus*, which has been accorded generic status by many modern authors (see Reig 1987, and Macedo and Mares 1987, for the history of the concept). It is even more strongly differentiated from *Akodon* (s.s.) than is *Oxymycterus* (mean D_R = 0.429; Table 4). *Chroeomys* is characterized by 17 unique alleles, nine of which are fixed (Table 5).
6. *Lenoxus* is the most strongly differentiated supraspecific taxon, with genetic distances to all others ranging from 0.538 to 0.764. Moreover, it is as divergent in comparison to *Oxymycterus* as it is to the other sampled genera (Table 4). These very large genetic distances are the result of 14 unique alleles (out of a total of 28) at 13 of the 26 loci examined; that is, fully 50 percent of the measured genome of *Lenoxus* is unique.
7. These taxa of akodontines are generally characterized by alleles either that are broadly shared among taxa or that uniquely define them. For example, four of the 26 loci examined exhibit a common allele shared by all taxa (Ldh-1, Mdh-1, Pgm, and Sod) and an additional 11 loci show a common allele shared by more than 10 of the taxa examined (Ldh-2, Ck-1, -2, Got-2, Icd-2, Mdh-2, Mpi, Sdh, 6Pgd, Pap, and Gd). On the other hand, of the total of 118 alleles detected, 68 of these (58.6 percent) are unique to single species.

Relationships among akodontine rodents

The relationships among this set of akodontine taxa suggested by these data are provided in figures 1 and 2 which represent, respectively, phenetic and phyletic perspectives based on genetic distances. The topologies of these trees are strongly concordant, with a single exception. In both cases, *Microxus* is placed within the complex of species that represent *Akodon* (s.s.), and *Akodon (Chroeomys)* is placed outside of a complex that includes *Akodon* (s.s.) and *Bolomys amoenus*. *Lenoxus* is placed outside of all the other taxa based on mid-point rooting; it does not form an identifiable unit with *Oxymycterus*. The only topological disagreement between these two views of relationships resides in the placement of the unnamed species of *Akodon* (s.s.) from central Peru. In the phenogram, it is the most differentiated member of *Akodon* (s.s.), while in the Wagner tree it is coupled with *subfuscus* and *puer* relative to all others. Note that in the Wagner tree, the branch lengths leading to the terminal taxa are approximately the same, indicating that the degree of accumulated molecular divergence has been relatively constant across lineages. Only *Lenoxus* seems to stand apart, but, as its placement is based on mid-point rooting, the actual length of the branch leading to it remains uncertain.

The high proportion of either broadly shared (= common) or unique alleles makes the documentation of any internal branching hierarchy among these taxa difficult at best (Fig. 3). For example, there are no alleles that uniquely define the seven species of *Akodon* (s.s.) as a group relative to other supraspecific taxa, and only three that so define *Oxymycterus* (Table 5). On the other hand, *Lenoxus* has uniquely fixed alleles at 50 percent of the loci examined (13/26), and *Chroeomys* is similarly distinctive at 34.5 percent of its loci (9/26). As a result, any character-state analysis will produce a large number of equally parsimonious trees, and resolution of relationships among these taxa supportive of the trends observed in the phenetic and Wagner distance procedures is not possible. Results of the various PAUP analyses, however, are informative. For example: 1. Every tree, regardless of the specified out-group taxon (or group of taxa), places *Microxus* as a member of a clade otherwise composed only of species of *Akodon* (s.s.). 2. It is not possible to identify *Microxus* as part of an out-group relative to *Akodon* (s.s.) without making the specified in-group polyphyletic (see also Hinojosa et al. 1987). 3. Equal length trees are produced when *Lenoxus, Oxymycterus, Bolomys,* or *Chroeomys* are designated as

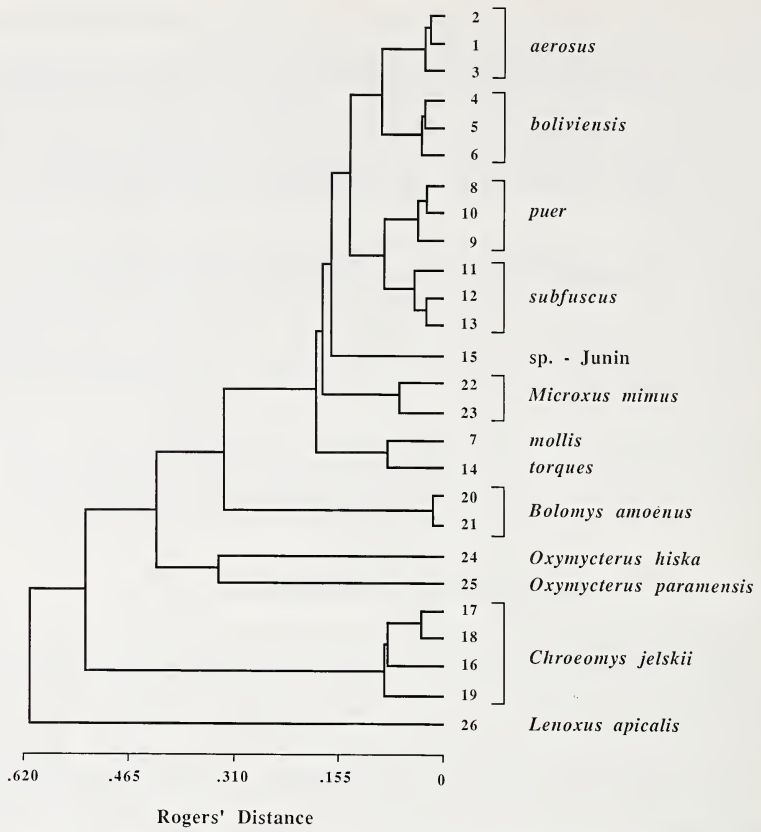

Fig. 1. UPGMA dendrogram of Rogers' (1972) genetic distance (D_R) for thirteen species and six supraspecific groups of akodontine rodents. Taxa not identified to genus are all members of *Akodon* (s. s.). Geographic localities for each taxon are indicated by number, as in the Specimens Examined section. Cophenetic correlation coefficient = 0.982

the out-group taxon. But, 4. a combination of *Oxymycterus* and *Lenoxus* (members of Hershkovitz' [1966] oxymycterine group) cannot be specified as an out-group together while, at the same time, retaining the remaining taxa as a monophyletic in-group (contra the more limited analysis presented in Hinojosa et al. 1987).

A concensus tree summarizing relationships among these six supraspecific taxa of akodontine rodents is given in Fig. 3. *Akodon* (s.s.) and *Microxus* are linked by two uniquely shared alleles, and a clade composed of all taxa with the exception of *Lenoxus* is identifiable by three shared alleles. However, it is not possible on the basis of character states alone to link *Bolomys, Chroeomys*, and *Oxymycterus* other than in a multichotomous fashion. Although these taxa exhibit quite different overall genetic distances both to *Akodon* (s.s.) and *Microxus* or to *Lenoxus*, these distances are the result of unique alleles along each branch, not shared ones that couple them in some hierarchical fashion.

Discussion

Akodontine rodents comprise a group of 10 genera and some 62 species (following Reig 1986). The most polytypic of these is the genus *Akodon*, for which Reig (1986) recognizes

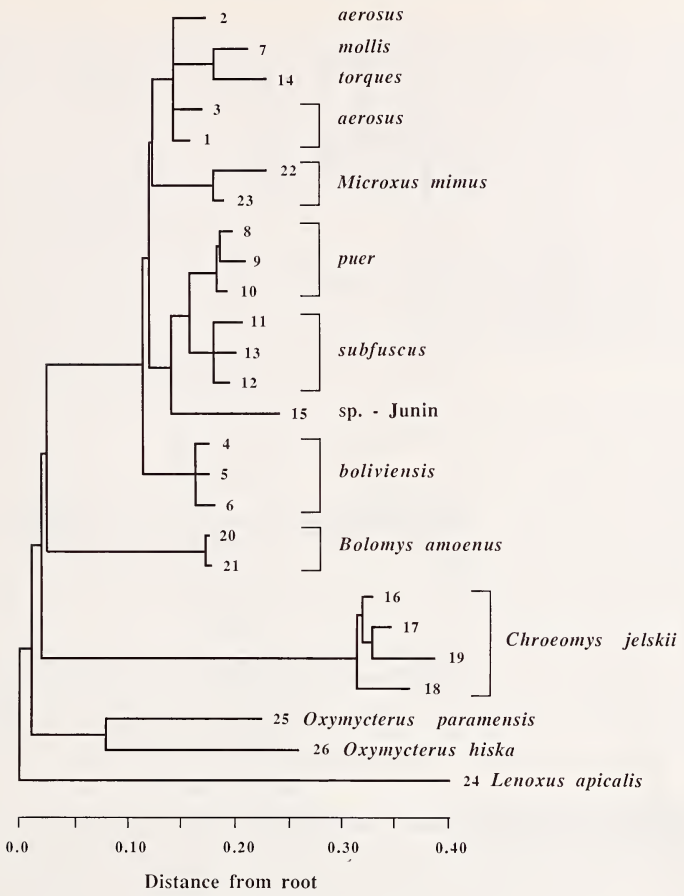

Fig. 2. Distance Wagner tree based on Rogers' genetic distance for thirteen species and six supraspecific groups of akodontine rodents (see Fig. 1). The tree was rooted by designating *Lenoxus* as an out-group taxon. Total tree length = 2.260; cophenetic correlation coefficient = 0.993

five subgeneric assemblages (*Akodon* s.s., *Abrothrix, Deltamys, Hypsimys*, and *Chroeomys*). While authors vary as to the explict taxa they recognize, and at what categorical level, no author has seriously questioned the monophyletic nature of the group. Rather, discussions associated with the akodontines have focused on 1. how many subgeneric groups of *Akodon* to recognize, and whether some of these should be recognized at the generic level; 2. whether *Zygodontomys* is an akodontine or not, and 3. whether the oxymycterines should be segregated as a group distinct from other akodontines, but annectant to them (e.g. Hershkovitz 1966). Reig (1987) provides a valuable synopsis of the history of the concept of the akodontines, and there is no need to repeat these remarks here. Hinojosa et al. (1987) review the question of an oxymycterine as opposed to an akodontine group and conclude that the definition of such is inconclusive with present information.

With the data presented above, we cannot address the issue of monophyly of an akodontine clade relative to other sigmodontines, as the analysis did not include any taxa outside of the akodontines as defined by Reig and other workers. We can, however, evaluate a set of hypotheses that previous authors have presented relative to relationships

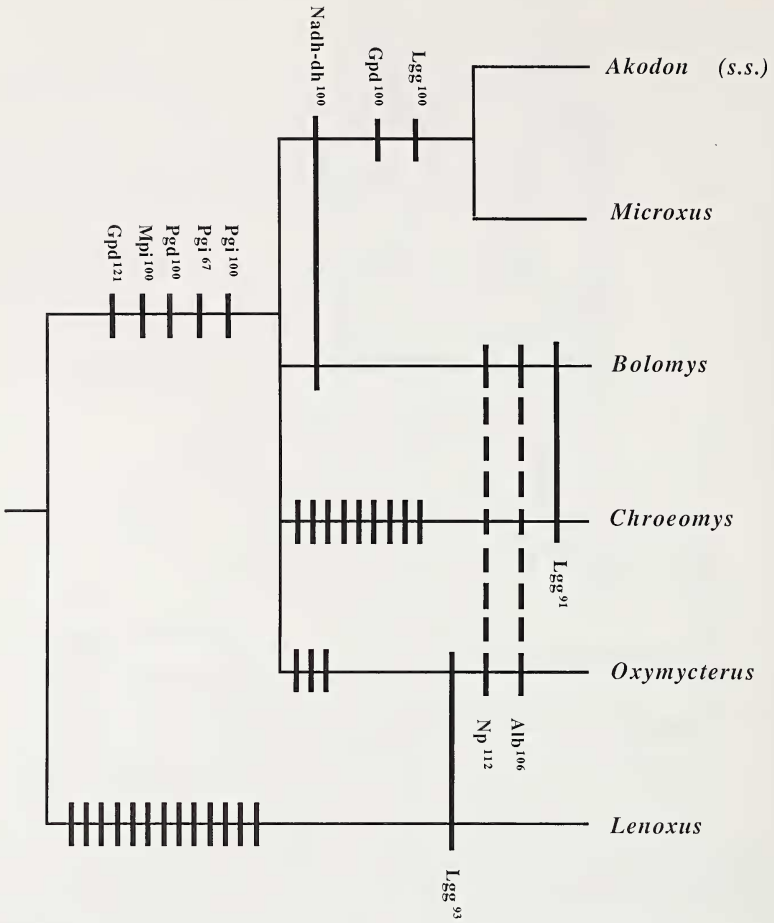

Fig. 3. A generalized cladogram for six supraspecific groups of akodontine rodents based on electromorph (= allele) distribution patterns. Alleles uniting pairs or groups of taxa are identified; those that uniquely define terminal taxa are indicated only as horizontal bars. See text for further discussion, and Table 5 for a list of allelic states for each taxon

within the akodontine group and, based on these evaluations, we can provide arguments for the hierarchical classification of the taxa that we have examined.

As Reig's (1987) synopsis of the history of the concept of the Akodontini reveals, there has been, and continues to be, much confusion as to the number of supraspecific units and of their suggested relationships. As a case in point, Hershkovitz (1966) included *Microxus* with *Abrothrix* in an oxymycterine group apart from the akodonts, while most prior and subsequent authors continue to recognize *Microxus* as a separate genus of akodonts and *Abrothrix* as a subgenus of *Akodon*. A similar history surrounds the supraspecific taxon *Bolomys* (see Macedo and Mares 1987). This state of affairs exists because supraspecific taxa (generic and subgeneric groups) are poorly defined within the akodontines. It is frankly not clear whether the lack of definition is real, in that it reflects only subtle differences among clades that diverged nearly simultaneously from a common ancestor resulting in taxa composed of a combination of primitively shared and uniquely derived characters, or whether the lack of a good definition now simply results from the fact that

no thorough analyses of character variation has been accomplished for all presumptive members of the group. For example, GARDNER and PATTON's (1976) compilation of chromosomal data provides a systematic view for only 5 of the 15 supraspecific groups of REIG (1986, 1987). Similarly, CARLETON's (1973) analysis of stomach morphology among the New World cricetines involves only four of these groups; and VOSS and LINZEY's (1981) study of the male reproductive tract examines but six. As useful as these studies are, the paucity of the available data means that substantive conclusions about supraspecific limits cannot be drawn as yet.

Our study suffers from the same faults as prior ones; it encompasses an inadequate number of akodontine taxa for a full view of the diversity of the group, and of the phyletic relationships of its components. Nevertheless, there are some firm conclusions that come from these data with regard to the hierarchical placement of several of the supraspecific taxa generally placed within this group. These inlcude:

1. *Microxus* (as represented by topotypic material of the type species, *mimus*) is at best a sister group to *Akodon* (s.s.), and perhaps will be found to have its place within that group. Certainly, it is more closely related to *Akodon* than is either *Chroeomys* or *Bolomys*, two supraspecific taxa that have been recognized as genera or subgenera of *Akodon* (THOMAS 1916, 1918; ELLERMAN 1941). The suggestion of HERSHKOVITZ (1966) that *Microxus* is an oxymycterine, not an akodont, is certainly not supported by the electromorphic data presented here or by a review of morphological characters (see HINOJOSA et al. 1987). His further argument that *Microxus* is an *Abrothrix* cannot be evaluated here; no other taxa allocated to *Abrothrix* were examined by us. We suspect, based on examination of specimens of the three species usually allocated to *Microxus* (*mimus*, the type species, *latibricola*, and *bogotensis*) is that *mimus* bears no relationship to the other two. Hence, the opinions of authors, such as REIG (1987), that *Microxus* stands apart from other akodontines may well rest on their view that *bogotensis* adequately represents the genus. It probably does not, and these species should be redefined relative to *Microxus mimus*.
2. *Chroeomys* is at least as equally divergent as is *Bolomys* (as represented by the type species *amoenus*) and, apparently, *Oxymycterus* relative to *Akodon* (s.s.). If *Bolomys* is to be recognized at the generic level, as most recent authors have done (see REIG 1987, for formal diagnosis of the genus *Bolomys*), then so must *Chroeomys* if paraphyletic taxa are to be disallowed, a philosophy to which we agree. This view is consistent with a general overview of the morphological and chromosomal position of *Chroeomys* made recently by SPOTORNO (1986).
3. *Lenoxus* is the most strongly differentiated taxon examined here, and it does not have a close relationship with any other akodontine. Judging by the number of unique alleles, it has had a long history of separation. Certainly, it is not close to *Oxymycterus* (following HERSHKOVITZ 1966), and it cannot be considered just a large version of that genus (REIG 1980, 1987). Nevertheless, it does have the highly specialized discoglandular stomach, very similar in morphology to that of *Oxymycterus* as described by CARLETON (1973; PATTON unpubl. data). Comparisons to genera outside of the akodontines are necessary to determine if *Lenoxus* and *Oxymycterus* are sister-taxa; i.e., its relationships may lie with *Oxymycterus*, but, if so, the divergence was near the basal radiation of the entire group.
4. The addition of other taxa, both the remaining genera and subgenera as well as a greater representation of speciose genera such as *Oxymycterus* and *Akodon*, will undoubtedly help resolve the relationships suggested herein. However, the general patterns detailed here suggest that most genera had their origins nearly simultaneously from a common ancestral stock(s). This view is supported by the dual facts that these taxa share a large number of alleles across the loci examined while simultaneously they are individually characterized by unique alleles. The pattern of electromorphic divergence, therefore,

mirrors the conclusion of Voss and Linzey (1981) regarding features of the male reproductive tract: evolution within the South American cricetines, as exemplified by the akodontines discussed herein, has likely been by ". . . rapid cladistic proliferation".

Acknowledgements

We thank Monica Frelow and Jennifer Talbot for help with all aspects of the laboratory analysis, and Carol Patton, John Cadle, Bob Jones, Michael Nachman, and Elena Vivar P. for aid in the collection of specimens. Oliver Pearson read an early draft of the paper and improved its contents based on his extensive personal experience with these rodents. Logistical support in Peru was provided by Tony Luscombe, Mari Figueroa, Renato Marin, and the Museo Historia Natural "Javiar Prado", and collecting permits were kindly supplied by the Ministerio de Agricultura, Lima. Financial support was provided by the National Geographic Society, the National Science Foundation, the Museum of Vertebrate Zoology, and the Rackham Foundation of the University of Michigan.

Zusammenfassung

Elektrophoretische Variabilität bei ausgewählten südamerikanischen akodontinen Nagetieren (Muridae: Sigmodontinae), mit Anmerkungen über Folgerungen zur Systematik

Die phylogenetischen Beziehungen zwischen 14 Arten aus 5 Gattungen südamerikanischer muroider Nager der Tribus Akodontini wurden mit Hilfe des gelelektrophoretischen Vergleichs von 26 Proteinen untersucht. Die Hauptergebnisse sind: 1. *Microxus mimus*, die Typus-Art der Gattung *Microxus*, kann nicht von *Akodon*-Arten aus der Untergattung *Akodon* unterschieden werden. 2. *Bolomys amoenus* unterscheidet sich genetisch nur wenig von *Akodon* (s.s.) und *Microxus mimus*. 3. *Akodon (Chroemys) jelskii* weicht sehr von allen anderen Akodontinen ab. Die Art besitzt an 9 der 26 untersuchten Loci nur bei ihr gefundene Allele. Sie ist mit Arten der Gattung *Akodon* (s.s.) nicht eng verwandt und sollte in eine eigene Gattung gestellt werden. 4. Am stärksten differenziert ist *Lenoxus apicalis*. 13 der 26 untersuchten Loci besitzen ausschließlich eigene Allele. Entgegen der Ansicht mancher Autoren bildet *Lenoxus* mit *Oxymycterus* keine monophyletische Gruppe.

Resumen

Las relaciones filogenéticas entre 13 especies y 5 generos de roedores muroideos sudamericanos de la Tribu Akodontini se examinaron mediante electroforesis de 26 loci proteicos. Los principales hallazgos incluyen: 1. El género *Microxus*, representado por la especie tipo *mimus*, es indistinguible de los taxa de *Akodon* (subgenero *Akodon*). 2. *Bolomys*, representado por la especie tipo *amoenus*, sólo se diferencia ligeramente de *Akodon* (s.s.) y *Microxus*, tanto en distancia genica como en el número de alelos diagnósticos. 3. *Akodon (Chroeomys) jelskii* es muy diferente de todos los otros akodontinos, con alelos diagnósticos en 9 de los 26 loci examinados; este taxón no puede considerarse pariente cercano de *Akodon* (s.s.) y debería reconocerse al nivel de género. Y 4. *Lenoxus apicalis* es el akodontino mas divergente con alelos diagnósticos en la mitad de los loci estudiados; este taxón no forma un clado con *Oxymycteros* como algunos autores han sugerido.

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